

## EFFECTS OF HUMAN RECREATION ON THE INCUBATION BEHAVIOR OF AMERICAN OYSTERCATCHERS

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**ABSTRACT.**—Human recreational disturbance and its effects on wildlife demographics and behavior is an increasingly important area of research. We monitored the nesting success of American Oystercatchers (*Haematopus palliatus*) in coastal North Carolina in 2002 and 2003. We also used video monitoring at nests to measure the response of incubating birds to human recreation. We counted the number of trips per hour made by adult birds to and from the nest, and we calculated the percent time that adults spent incubating. We asked whether human recreational activities (truck, all-terrain vehicle [ATV], and pedestrian traffic) were correlated with parental behavioral patterns. Eleven *a priori* models of nest survival and behavioral covariates were evaluated using Akaike's Information Criterion (AIC) to see whether incubation behavior influenced nest survival. Factors associated with birds leaving their nests ( $n = 548$ ) included ATV traffic (25%), truck traffic (17%), pedestrian traffic (4%), aggression with neighboring oystercatchers or paired birds exchanging incubation duties (26%), airplane traffic (1%) and unknown factors (29%). ATV traffic was positively associated with the rate of trips to and away from the nest ( $\beta_1 = 0.749$ ,  $P < 0.001$ ) and negatively correlated with percent time spent incubating ( $\beta_1 = -0.037$ ,  $P = 0.025$ ). Other forms of human recreation apparently had little effect on incubation behaviors. Nest survival models incorporating the frequency of trips by adults to and from the nest, and the percentage of time adults spent incubating, were somewhat supported in the AIC analyses. A low frequency of trips to and from the nest and, counter to expectations, low percent time spent incubating were associated with higher daily nest survival rates. These data suggest that changes in incubation behavior might be one mechanism by which human recreation affects the reproductive success of American Oystercatchers. Received 28 July 2005, accepted 24 April 2006.

The effect of human recreational activity on wildlife is an increasingly important area of research (Burger 1981, Burger and Gochfeld 1998, Fitzpatrick and Bouchez 1998, Whittaker and Knight 1998, Carney and Sydeman 1999). Human disturbance has been linked to altered foraging behavior (Burger 1981, Burger and Gochfeld 1998, Fitzpatrick and Bouchez 1998, Rodgers and Schwikert 2003, Stolen 2003) and diminished reproductive success of many waterbird species (Hunt 1972, Robert and Ralph 1975, Tremblay and Ellison 1979, Safina and Burger 1983, Rhulen et al. 2003). The mechanisms by which human disturbance lowers reproductive success, however, are poorly understood.

Current data indicate that American Oys-

tercatcher (*Haematopus palliatus*) populations in the Mid-Atlantic states are declining (Mawhinney and Benedict 1999, Davis et al. 2001). The U.S. Shorebird Conservation Plan lists the American Oystercatcher as a "Species of High Concern," due, in part, to human encroachment on breeding habitat (Brown et al. 2001). Evidence that humans are directly responsible for American Oystercatcher nest failure is limited (Davis et al. 2001, McGowan 2004); however, human recreation is often associated with lower oystercatcher reproductive success (Hockey 1987, Jeffery 1987, Novick 1996, Davis 1999, Leseberg et al. 2000, Verhulst et al. 2001, McGowan 2004). Because American Oystercatcher populations may require intensive management in the near future, it is important to understand the relationship between human recreation and oystercatcher nesting success (Brown et al. 2001, Davis et al. 2001).

Skutch (1949) hypothesized that higher levels of parental activity during the nesting period might lead to greater rates of predation because more activity makes nests more obvious to predators. Because American Oystercatchers are ground-nesting shorebirds that are easily flushed from their nests (Davis 1999),

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we similarly hypothesized that human recreation might increase the activity of incubating oystercatchers, thereby leading to increased predation rates. Although Skutch's hypothesis has been tested extensively, conclusions are mixed (Martin 1992, Roper and Goldstein 1987, Martin et al. 2000, Tewksbury et al. 2002). We believe that nesting American Oystercatchers provide a good opportunity to test Skutch's hypothesis because their nests are relatively easy to find and monitor, and they experience high rates of nest predation (Nol and Humphrey 1994, Davis et al. 2001, Sabine et al. 2005).

In this study, we used video monitoring to record human recreational activity and the behavior of incubating oystercatchers nesting on the Outer Banks of North Carolina. We asked whether human recreational activity altered the behavior of nesting birds, and whether increased parental activity or decreased nest attendance were associated with higher rates of nest failure.

## METHODS

*Study areas.*—We monitored nesting success of American Oystercatchers at Cape Lookout (76° 32' W, 34° 36' N) and Cape Hatteras (75° 31' W, 35° 24' N) national seashores in North Carolina during 2002 and 2003. The seashores comprise >160 km of barrier island habitat that supports ~90 breeding pairs of American Oystercatchers. All work at Cape Lookout National Seashore was conducted on North Core Banks and South Core Banks (see Godfrey and Godfrey 1976 for site description). Cape Hatteras National Seashore comprises three main islands: Bodie, Hatteras, and Ocracoke Islands. These barrier islands are long, narrow, and bordered by sandy beaches on the ocean side and salt marshes on the sound side. American Oystercatchers nest on the ocean side beaches, dunes, and adjacent sand flats. Raccoons (*Procyon lotor*) and feral cats (*Felis catus*) are common on all islands except Ocracoke, which has no raccoons. The islands are open to the public and most beaches are open to vehicles. Approximately 650,000 people visit Cape Lookout each year; the visitation rate at Cape Hatteras is considerably higher and has increased steadily from 1.5 million in 1986 to 2.2 million in 2005 (National Park Service 2005). Park visitors

use the beaches for walking, shell collecting, swimming, and fishing, and they drive four-wheel drive passenger vehicles (ORVs) and smaller, all-terrain vehicles (ATVs) on the beach. Vehicles are permitted along a network of unpaved roads behind the primary dunes and anywhere on the open beach, except in designated areas that are closed to protect vegetation, nesting sea turtles, and shorebirds, and to prevent erosion.

*Data collection.*—We located oystercatcher nests ( $n = 268$ ) and, from 15 April until 30 July in 2002 and 2003, checked their status every 3–4 days until chicks hatched or the nests failed. We used SONY HI-8 video cameras to record the incubation behavior of nesting adults at randomly selected nests ( $n = 72$ ). We videotaped nests on Bodie Island and Hatteras Island (Cape Hatteras National Seashore), and on North Core Banks and South Core Banks (Cape Lookout National Seashore). Nests were filmed for approximately 4-hr intervals at least once between the completion of egg laying and hatching. In the absence of human recreational activity, we assumed that parental behavior would be natural and homogenous throughout the incubation period. Evidence indicates that both American and Black (*Haematopus bachmani*) oystercatchers incubate their eggs 90–100% of the time once the clutch is completed, and that the amount of time spent incubating does not vary during the incubation period (Nol and Humphrey 1994, Andres and Falxa 1995). Verboven et al. (2001) showed that Eurasian Oystercatchers incubated 85–90% of the time at undisturbed nests, and that the percentage of time spent incubating was constant between the end of the laying period and hatching. Studies of other shorebird species indicate similar incubation patterns (Norton 1972), although Cartar and Montgomerie (1987) found that nest attendance of White-rumped Sandpipers (*Calidris fuscicollis*) may vary daily, depending on weather or other environmental factors.

Novick (1996) reported that human activity on South Core Banks at Cape Lookout National Seashore was distributed "fairly evenly" throughout the day and was greater on weekends (Friday–Sunday) than on weekdays. Novick (1996) also reported that humans concentrated around activity centers, such as the

ferry dock, the lighthouse, and the ocean inlets at the north and south ends of South Core Banks. Our nests were filmed between 07:00 and 14:00 EST, on both weekdays and weekends, which we believe provided an unbiased representation of human disturbance and parental activity patterns at each nest.

Each video camera was housed in a weatherproof plastic container attached to a metal stand, and placed approximately 5 m from the nest to avoid disturbing incubating birds. Most cameras faced the ocean and recorded activity both in the vicinity of the nest and on open beach beyond the nest. Sometimes cameras were placed at nests located in the dunes or other locations where the ocean-side beach was not visible. In these cases, we directed cameras toward the most likely source of human recreation (e.g., the dune road at Cape Lookout). The area sampled by the video camera was different for each nest due to differences in the surrounding landscape; therefore, detection probabilities for human activities were heterogeneous among nests. We reviewed tapes in real time to count the number of trips by incubating birds to and from the nest per hr, and the percent time that adults spent incubating. Herein, the term "trip" refers to a bird leaving or returning to its nest. We also counted the number of ORVs, ATVs, and/or pedestrians passing each nest per hr.

*Statistical analyses.*—We used the Mayfield (1961, 1975) method to estimate daily nest survival rates and hatching success for all nests monitored. We applied the Mayfield estimate to entire clutches and did not consider individual egg survival. Heterogeneity in survival probabilities during the incubation stage was not considered, and the midpoint rule was used to designate the time of failure and time of hatching for nests that failed or hatched between visits. We considered nests successful if at least one egg hatched, and failed when all eggs were lost. Partial nest failure was not considered in this study.

Each time a bird left its nest we estimated the time between departure and the time at which the probable causal event occurred. Possible causal factors included: ATV, ORV, pedestrian, and airplane traffic, as well as interactions between territorial pairs and exchanges in incubation duties. We report these data as the percent of nest departures for

which one of the above causal factors followed. We also report the percent of observed human recreational activities that were preceded by a bird leaving its nest.

We used linear regression models (Neter et al. 1996) to determine whether human recreational factors were correlated with oystercatcher parental activity. Trips per hr and percent time spent incubating were modeled as dependant variables, with number of ORVs, ATVs, and pedestrians passing a nest per hr serving as the independent variables.

For camera-monitored nests, we used the logistic exposure method to estimate daily nest survival (Shaffer 2004). We used SAS (ver. 9.1; SAS Institute, Inc. 2003) to generate survival estimates and to test competing models of nest survival with parental behaviors as covariates (Shaffer and Thompson in press). We tested 11 *a priori* models (Table 1) that modeled trip rate and percent time incubating as both continuous and categorical variables. We used two methods for categorizing the data: one purely statistical and one based on behavioral observations. For statistical categorical models, we split the data for number of trips/hr (Tripcat) and percent time incubating (Inccat) into low and high categories, using the median value of each as the cut-off point (Tripcat1:  $\leq 3.69$  trips/hr = low,  $> 3.69$  trips/hr = high; Inccat1:  $\leq 85\%$  = low,  $> 85\%$  = high). For the second method (biological categorical models), we used the average values from seven nests that had no evidence of human disturbance; we then divided the data into a new set of low and high categories. In this case, undisturbed nests averaged 2.25 trips per hr. Therefore, we used three trips per hr as a conservative estimate of oystercatcher nest site activity in the absence of human disturbance (Tripcat2:  $\leq 3.0$  trips/hr = low,  $> 3.0$  trips/hr = high). Time spent incubating by undisturbed birds averaged 90% of the observation period; thus, we used 90% as the cut-off point to categorize nests as low or high in terms of percent time spent incubating (Inccat2:  $\leq 90\%$  = low,  $> 90\%$  = high). We modeled each categorical variable separately and in a model that included both trip rate and percent time incubating (Table 1). One model included a year effect, and we tested a null model (null) that assumed constant survival over the season. We used an information the-



TABLE 1. Eleven candidate models used to examine the relationship between daily nest survival and parental incubation behaviors of American Oystercatchers nesting on the Outer Banks of North Carolina in 2002 and 2003.

Candidate model	Model covariates
Global Continuous	Year, trips to and from the nest per hr, percent incubation time
Year	Year
Models with statistically categorized data (splitting low and high data at the median value)	
Global categorization 1	Year, tripcat1, inccat1 <sup>a</sup>
Tripcat1 + inccat1	Tripcat1, inccat1
Tripcat1	Tripcat1
Inccat1	Inccat1
Models with biologically categorized data (splitting data at the average value for undisturbed nests)	
Global categorization 2	Year, tripcat2, inccat2
Tripcat2 + inccat2	Tripcat2, inccat2
Tripcat2	Tripcat2
Inccat2	Inccat2
Null	No covariates, assumes constant survival

<sup>a</sup> Inccat1, inccat2, tripcat1, and tripcat2 are categorical variables into which nests were categorized as low or high in terms of percent time adult birds spent incubating (inccat) or the number of trips adults made to and from the nest/hr (tripcat), according to the criteria that follow: inccat1:  $\leq 85\%$  = low,  $> 85\%$  = high; inccat2:  $\leq 90\%$  = low,  $> 90\%$  = high; tripcat1:  $\leq 3.69$  trips/hr = low,  $> 3.69$  trips/hr = high; tripcat2:  $\leq 3.0$  trips/hr = low,  $> 3.0$  trips/hr = high.

oretic approach to rank the models from most to least supported, based on Akaike's Information Criterion (AIC)—using  $AIC_c$ ,  $\Delta AIC_c$ , and Akaike weights ( $w_i$ ); Burnham and Anderson 2002). Means are reported  $\pm$ SE.

## RESULTS

We monitored 185 nests at Cape Lookout and 83 nests at Cape Hatteras. The overall Mayfield estimate of daily nest survival was  $0.92 \pm 0.006$  at Cape Lookout and  $0.94 \pm 0.007$  at Cape Hatteras. The highest daily nest survival rates were recorded at Cape Hatteras in 2003 ( $0.96 \pm 0.008$ ), and the lowest were recorded at Cape Lookout in 2002 ( $0.90 \pm 0.007$ ); these were the only year and location comparisons that were significantly different ( $Z = 4.83$ ,  $P < 0.001$ ).

We filmed 72 nests for a total of 320.18 hr and a mean of  $4.45 \pm 1.19$  hr per nest. Most nests were filmed once for  $\sim 4$  hr, but some were filmed twice before they hatched or failed. We excluded one nest from the analysis where it appeared that the bird's behavior was affected by the presence of the video camera. Of the 72 nests filmed, chicks successfully hatched from 19 and 53 nests failed. Sixty two percent of nest failures were due to mammalian predation ( $n = 32$ ), 28.5% failed for unknown reasons ( $n = 15$ ), and 11% were lost

to weather, human destruction, or abandonment ( $n = 6$ ).

Though not true experimental controls, there were seven nests at which we observed no human disturbance during filming. Birds at those nests incubated for  $90\% \pm 0.033$  of the filming period and made  $2.25 \pm 0.60$  trips/hr compared to  $82\% \pm 0.017$  incubation and  $3.66 \pm 0.17$  trips/hr at all other nests. The number of trips/hr at undisturbed nests was significantly lower ( $t = 2.27$ ,  $P = 0.026$ ) than at all other nests. The percent of time spent incubating at undisturbed nests was not significantly greater ( $t = 1.34$ ,  $P = 0.19$ ) than it was at disturbed nests.

We recorded 539 instances in which incubating birds departed their nests. Of those instances, ATVs were filmed within 3 min of nest departure on 136 occasions (25%) and ORVs were filmed 92 times (17%) within 3 min of departure. We recorded a total of 284 ATVs, 62% ( $n = 177$ ) of which passed by a nest within  $< 3$  min of a bird departing its nest. We observed 1,466 ORVs pass by filmed nests, but only 11% ( $n = 168$ ) passed by within 3 min of a bird leaving its nest. Groups or individual pedestrians were filmed 19 times (4%) within 10 min of nest departures. Of all the 110 pedestrians that we observed, 33% ( $n = 36$ ) passed by within 10 min of a bird de-

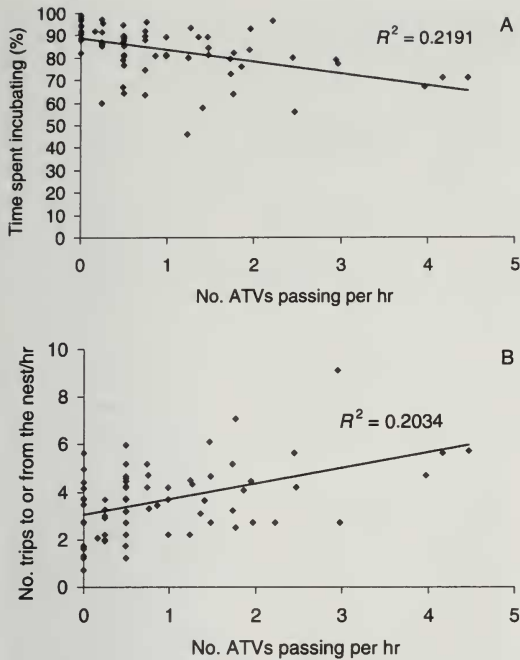


FIG. 1. The effect of all-terrain vehicle (ATV) beach traffic on incubation behavior of American Oystercatchers on the Outer Banks of North Carolina during the 2002 and 2003 breeding seasons: (A) relationship between the percent of time spent incubating and the average number of ATVs passing per hour ( $\beta_1 = -0.037$ ,  $P = 0.025$ ), and (B) relationship between the number of trips to and from the nest per hr and the number of ATVs passing per hr ( $\beta_1 = 0.749$ ,  $P < 0.001$ ).

parting its nest. Eight percent ( $n = 44$ ) of nest departures were associated with territorial disputes and 18% ( $n = 108$ ) with the exchange in incubation duties. Eight departures (1%) were associated with low-flying airplanes that passed within 3 min of nest departure. For the remaining 29% ( $n = 154$ ) of nest departures, no disturbances, territorial interactions, or incubation exchanges took place following departure.

Regression models showed that there was little or no association between ORV traffic and the rate at which incubating oystercatchers made trips to and from their nests ( $\beta_1 = 0.018$ ,  $P = 0.064$ ) or the percent time they spent incubating ( $\beta_1 = 0.0006$ ,  $P = 0.57$ ). Likewise, pedestrian traffic was not associated with a significant reduction in the percent time incubating ( $\beta_1 = -0.005$ ,  $P = 0.75$ ) or birds making more trips to and from their nests per hr ( $\beta_1 = -0.268$ ,  $P = 0.079$ ). Increased ATV traffic, however, was associated with a reduction in the percent time spent incubating ( $\beta_1 = -0.037$ ,  $P = 0.025$ ) and an increase in the rate of trips to and from the nest ( $\beta_1 = 0.749$ ,  $P < 0.001$ ; Fig. 1).

All models except the global continuous model received some level of support, but no model had overwhelming support (Table 2). The tripcat2 model (i.e., nests divided into low and high categories based on average trip rate for nests with no observed human distur-

TABLE 2. Candidate models examining the relationship between daily nest survival and parental incubation behaviors of American Oystercatchers nesting on the Outer Banks of North Carolina in 2002 and 2003. Models are ranked in descending order of support based on Akaike's information criteria  $AIC_c$ ,  $\Delta AIC_c$ , and Akaike weights ( $w_i$ ).

Model	Log-likelihood	No. parameters	$AIC_c$	$\Delta AIC_c$	$w_i$
Tripcat2 <sup>a</sup>	-159.62	2	323.27	0.00	0.28
Null	-161.08	1	324.16	0.89	0.18
Tripcat2 + inccat2 <sup>a</sup>	-159.62	3	325.29	2.02	0.10
Inccat1	-160.68	2	325.39	2.11	0.097
Inccat2	-160.77	2	325.56	2.29	0.089
Tripcat1	-160.98	2	325.99	2.72	0.072
Year	-161.07	2	326.17	2.90	0.066
Tripcat1 + inccat1	-160.26	3	326.56	3.29	0.054
Global categorical2	-159.56	4	327.18	3.92	0.040
Global categorical1	-160.24	4	328.54	5.28	0.020
Global continuous	-261.36	4	530.79	207.52	0.000

<sup>a</sup> Inccat1, inccat2, tripcat1, and tripcat2 are categorical variables into which nests were categorized as low or high in terms of percent time adult birds spent incubating (inccat) or the number of trips adults made to and from the nest/hr (tripcat), according to the criteria that follow: inccat1:  $\leq 85\%$  = low,  $> 85\%$  = high; inccat2:  $\leq 90\%$  = low,  $> 90\%$  = high; tripcat1:  $\leq 3.69$  trips/hr = low,  $> 3.69$  trips/hr = high; tripcat2:  $\leq 3.0$  trips/hr = low,  $> 3.0$  trips/hr = high.

TABLE 3. Daily survival estimates and hatching probability estimates for nests in two categories of behavioral data collected from American Oystercatchers nesting on the Outer Banks of North Carolina in 2002 and 2003.

Category	No. nests	Daily probability of survival	Lower / upper confidence intervals	Hatching probability
Median cutoffs				
≤3.69 trips/hr	37	0.958	0.935 / 0.973	0.314
>3.69 trips/hr	35	0.948	0.925 / 0.965	0.240
Incubation ≤85%	32	0.961	0.938 / 0.975	0.338
Incubation >85%	40	0.945	0.922 / 0.962	0.218
Zero-observed-disturbance average cutoffs				
<3.00 trips/hr	26	0.969	0.946 / 0.982	0.424
>3.00 trips/hr	46	0.944	0.924 / 0.960	0.213
Incubation <90%	50	0.967	0.945 / 0.980	0.400
Incubation >90%	22	0.948	0.926 / 0.964	0.237

bance as the only covariate) had the highest rank of all the models ( $\Delta AIC_c = 0.00$ ,  $w_i = 0.28$ ). The null model was ranked second ( $\Delta AIC_c = 0.89$ ,  $w_i = 0.18$ ), and the model incorporating both *tripcat2* and *inccat2* was ranked third ( $\Delta AIC_c = 2.02$ ,  $w_i = 0.10$ ). All the models with categorical behavioral variables, the year model, and the null model had a  $\Delta AIC_c$  of <7 and weights between 0.02 and 0.28 (Table 2). Generally, models with a  $\Delta AIC_c$  of <7 cannot be ruled out, but models with weights <0.70 cannot be exclusively accepted (Burnham and Anderson 2002).

The estimated daily survival rate for nests with ≤3.69 trips to and from the nest per hr was greater than the daily survival rate for nests with >3.69 trips to and from the nest per hr (Table 3). That same pattern was observed when the data were divided into categories representing nests with ≤3 trips per hr and >3 trips per hr. Nests in which the parents incubated for ≤85% of the observation period had higher daily survival probabilities than nests in which incubation percentages were >85%. The same pattern was observed when we categorized the data by nests in which adults spent ≤90% and >90% time incubating. These data indicated that nests in which parents made more trips to and from the nest had a lower daily survival probability, and that nests where the parents spent more than 85–90% of their time incubating had a lower chance of surviving each day.

#### DISCUSSION

Our data show clear associations between human recreation and incubation behavior of

American Oystercatchers. ATV traffic was associated with increased rates of trips to and from the nest and reduced time incubating; other forms of human recreation were more weakly associated with oystercatcher nesting behaviors. Sixty two percent of the ATVs that we observed passed within 3 min of a bird departing its nest, whereas the same was true for only 11% of the ORVs that we observed. Birds appear to have habituated to the presence of ORVs (Whittaker and Knight 1998), but they view ATVs (and to a lesser extent, pedestrians) as threats. Peters and Otis (2005) reported that wintering American Oystercatchers habituated to boat traffic on the intercoastal waterway in South Carolina. Other studies have shown that birds respond differently to different forms of human recreational disturbance (Burger 1981), but most have focused only on changes in foraging behavior (Burger and Gochfeld 1998, Rodgers and Schwikert 2003, Stolen 2003). Our study is one of the few to investigate how human recreational disturbance affects incubation behavior. ATVs are louder and move faster than ORVs and pedestrians, which might explain why the birds are affected more by ATV traffic (Burger 1981, Burger and Gochfeld 1998). ORVs and pedestrians also tend to stay closer to the firm sand along the water's edge, which means they generally travel farther from nesting birds.

Although the probability of hatching was low in all nests, regardless of parental activity, we did find evidence that human recreational disturbance may reduce the nesting success of



American Oystercatchers by altering incubation behavior. Analyses based on AIC model selection indicated that the rate of parental trips to and from the nest and the percent time that parents spent incubating may have affected daily nest survival rates. Although no model received overwhelming support, none of the categorical behavioral models could be ruled out. The daily survival estimates indicated that nesting adults that made fewer trips to and from the nest had greater daily nest survival rates. Conversely, nests where the parents incubated for less time had higher daily survival rates. We hypothesize that mammalian nest predators, the primary nest predators in this system (Davis et al. 2001), are better able to find disturbed nests through smell because each time a parent gets up and walks away from a nest it leaves a scent trail that raccoons and cats may follow. Our results differ from those of Verboven et al. (2001), but that is likely because the primary nest predators in that system were avian predators.

ATV traffic is not the only factor affecting oystercatcher nesting success on North Carolina's Outer Banks. Nest predation is an important determinant of hatching success in the Outer Banks (Davis et al. 2001, McGowan et al. 2005), and relationships between human recreation and nest predators are poorly understood. Vehicular traffic also may affect success during the chick-rearing phase of reproduction. In the 2003 breeding season, we confirmed that five chicks from three different nests were run over by vehicles on the beaches of South Core Banks at Cape Lookout National Seashore and Hatteras Island at Cape Hatteras National Seashore (McGowan 2004).

The negative association between percent time incubating and daily nest survival seems counterintuitive. Conway and Martin (2000) showed that birds balance the costs of egg exposure with those of high parental activity. Birds with high levels of nest-predation pressure minimize nest-site activity by taking fewer, longer trips off the nest (Conway and Martin 2000). This behavior helps reduce parental activity around the nest, but it also reduces the amount of incubation. American Oystercatcher behavior may reflect a similar trade off; their eggs can tolerate extensive heating and cooling (Nol and Humphrey 1994). In our study, several clutches exposed for approxi-

mately 1 hr at mid day hatched successfully. One videotaped nest hatched successfully, even though the parents incubated for only 66.8% of the 4.07-hr observation period. Egg hardiness may reflect an adaptation that enables parents to reduce nest-site activity. Parents that depart their nest and wait until multiple disturbances have passed before returning may have greater nesting success than parents that return to their nests quickly and flush repeatedly. Future analyses should assess the effect that the average amount of time birds spend off the nest has on nest success.

There were several potential sources of measurement error in our study that might explain why no models were strongly supported. Incubation behavior might vary as birds habituate to disturbance (Whittacker and Knight 1998). Because the field of view varied at each nest, our cameras recorded areas of different size for each nest, and we were unable to control for these differences in the analyses. We were also unable to measure the distance from the nests to the disturbance recorded on our video. Several studies have shown that the proximity of human disturbance has a major effect on the behavioral responses of birds (Burger and Gochfeld 1998, Rodgers and Schwikert 2003). It is likely that in some cases, recreational activity recorded by our cameras did not elicit a response from the incubating bird because the activity was too far away. Video monitoring is an extremely useful tool for studying avian behavior; however, future studies of human disturbance using video monitoring should entail measuring distances to sources of disturbance. Recording nests for longer periods of time also would alleviate a great deal of uncertainty. Sabine et al. (2005) were very successful in studying nest success of oystercatchers in Georgia by using time-lapse videography throughout the incubation period.

Our simplified approach of categorizing nests into low or high levels of parental activity provided a coarse-scale observational measure of behavioral responses to recreation and disturbance; we expected this to reduce observation errors. Other researchers that have evaluated the effects of human disturbance on avian behavior used experimental designs with defined treatment groups (Robert and Ralph 1975, Tremblay and Ellison 1979, Ver-

hulst et al. 2001, Stolen 2003). We studied the effects of ambient human disturbance caused by park staff and recreational visitors to determine whether it was linked to patterns of nesting success. Future studies of human activity and oystercatcher nesting success that compare the behavior of birds on beaches closed to vehicle and pedestrian traffic with the behavior of birds exposed to different types and intensities of human activity are needed to improve our understanding of the patterns suggested by this study.

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